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SYNECOLOGICAL STUDY ON INTERTIDAL COMMUNITIES

I. THE ZONATION OF INTERTIDAL ANIMAL COMMUNITY WITH SPECIAL REFERENCE TO THE INTERSPECIFIC RELATION[1]

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(With one figure)

As the zonation of marine invertebrates within narrow vertical limits of the sea cliff is a striking feature, ecological investigations have been done by many authors. Some investigators have examined the relation between the animal zones and the environmental factors governing a certain locality, and the other workers tried to analyse the ecological succession in the intertidal region. It is interesting to notice that Stephenson and Stephenson (1949) suggested that the fundamental intertidal zonation is found universally.

Studies concerned with the environmental factors were carried out by the thought that the distribution of the intertidal animals may be limited by critical environmental factors. Though the intertidal community is classified into zones by various characteristic species, it is easily supposed that these species are not only arranged by the environmental conditions, but are also influenced by the biotic factors, so called "coaction". It is generally said that competition for space exists among them, and also that a change of the constituent species is often recognized. The ecological succession in the intertidal region had been noted by Hewatt (1935, 1937), Kanda (1947), Katada and Matsui (1953) and Newcombe (1935).

Nevertheless, the mechanism of the replacement in the constituent species is not yet sufficiently clarified. Therefore, the writer attempted to study the interrelation among the organinsms which appear in the forming process of zonation, and in the present paper an analysis of the zonation on the cliff face of a headland will be dealt with.

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SAMPLING METHOD

The headland, Tobi-ga-Saki, is situated near Matsushima Bay, Pacific coast of Miyagi Prefecture, northern part of Japan. The headland is composed of tuff and extends seawards from the sandy shore. The surface of the steep cliff is relatively smooth and faces south except for Sts. 1, 3 and 4.

Seven stations were selected for sampling from the beach towards the sea. For quantitative investigation, a belt (50 cm in width) was selected vertically on the cliff face in each station, and this was divided into horizontal belts at intervals of 10 cm above and below high water level. The horizontal belt (10×50 cm) is subdivided into five 10 cm squares. The individual number of the animals in each square were counted. In the case of two species of porifera, the percentage of the area covered by them was estimated.

The examination was carried out from May to June 1956. The seasonal change in the population of these animals was not so remarkable, thus the zonation was rather stable during this period. Only animals, especially sedentary animals were examined, because in the area studied no algal zone was found. In the vicinity of Matsushima Bay the characteristic sedentary animals which form the zones are: *Chthamalus challengeri* Hoek, *Balanus amphitrite albicostatus* Pilsbry, *Ostrea gigas* Thunberg, *Septifer virgatus* (Wiegmann), *Mytilus edulis* Linné, *Reniera japonica* Kadota and Sponge sp. 1.

As the distribution of the animals seems to correlate generally to the wave action, the intensity of it was studied. When the wave washes the cliff, three kinds of surf are recognized, viz. splash, breaker and brushing water. The degree of desiccation of the rock face during the tides in summer was also observed in relation with the distribution of the animals. Washing limits of each kind of surf during the high tide and also the drought part and wet one during the tides on a calm day, were noticed.

PHYSIOGNOMICAL DESCRIPTION

Station 1. The wave action is relatively weak, for the cliff faces west and is sheltered from the surging wave. The cliff is divided into two parts of splashing water and brushing water. The rock face dries up between the tides in summer. Zones of *C. challengeri*, *C. challengeri–O. gigas*, *B. a. albicostatus–O. gigas–M. edulis* and *M. edulis–B. a. albicostatus* arranged in the order from the upper part downwards were recognized.

Station 2. This station faces south and wave action is stronger than in St. 1. Here the feature of zonation is similar to that in St. 1, except for that *M. edulis* increases in number and in the patches of it *S. virgatus* appears.

Station 3. The strong wave washes the cliff which faces southeast. The cliff consists of the splashing water part and the breaker one. The rock face dries up between the tides in summer. From the upper part to the lower part, zones of *C. challengeri*, *C. challengeri–O. gigas*, *M. edulis–S. virgatus* and *B. a. albicostatus–O. gigas* are constructed. In the breaker part *M. edulis* and *S. virgatus* crowd remarkably.

Station 4. The environmental condition and zonation in this station are similar to that in St. 1. But *R. japonica* appears in the wet part.

Station 5. Here, the cliff faces south and the wave action is stronger than in St. 2, and splash raises upwards. The highest zone is dominated by *C. challengeri* and the next consists of *C. challengeri*, *B. a. albicostatus*, *O. gigas*, *S. virgatus* and *M. edulis*. Dominant species in the third zone are *O. gigas* and *R. japonica*. In the fourth zone *M. edulis* and *S. virgatus* dominate contrary to the decreasing of *O. gigas*. The fifth is the *M. edulis* zone and the lowermost one is the *O. gigas* zone.

Station 6. Waves wash the rock stronger than in the above-mentioned stations. In response to the strong splash the *C. challengeri* zone extends to the upper part. Under it the *M. edulis–S. virgatus* zone develops. The *M. edulis–R. japonica* zone follows it. The fourth zone consists of *M. edulis*. The lowest is the *O. gigas* zone.

Here, *B. a. albicostatus* disappears and *O. gigas* decreases in the upper part. In the wet part *R. japonica* and Sponge sp. 1 appear abundantly.

Station 7. The wave action is stronger than in St. 6. In spite of the raising of the upper limit of the distribution of *C. challengeri* which is accompanied with raising of the splash, the *C. challengeri* zone does not extend, for its lower limit raises. Under it *M. edulis* and *S. virgatus* form a remarkable zone. The Sponge sp. 1–*M. edulis* zone lies between the *M. edulis* zone and the *M. edulis–S. virgatus* zone. The lowest is the *O. gigas*–Sponge sp. 1 zone.

In this station *O. gigas* disappears from the upper part and *R. japonica* vanishes from the middle part.

NUMERICAL TREATMENT

In Fig. 1, the results of quantitative studies on the animals in each horizontal belt in Sts. 1, 3, 5 and 7 are represented by the black bars. As shown in Fig. 1, the obtained results correspond with the above-mentioned physiognomical descriptions.

The noteworthy features recognized are the following:

1. Accompanied with the raising of the upper limit of the splash area the range of the distribution of *C. challengeri* extends upwards, but this zone can be

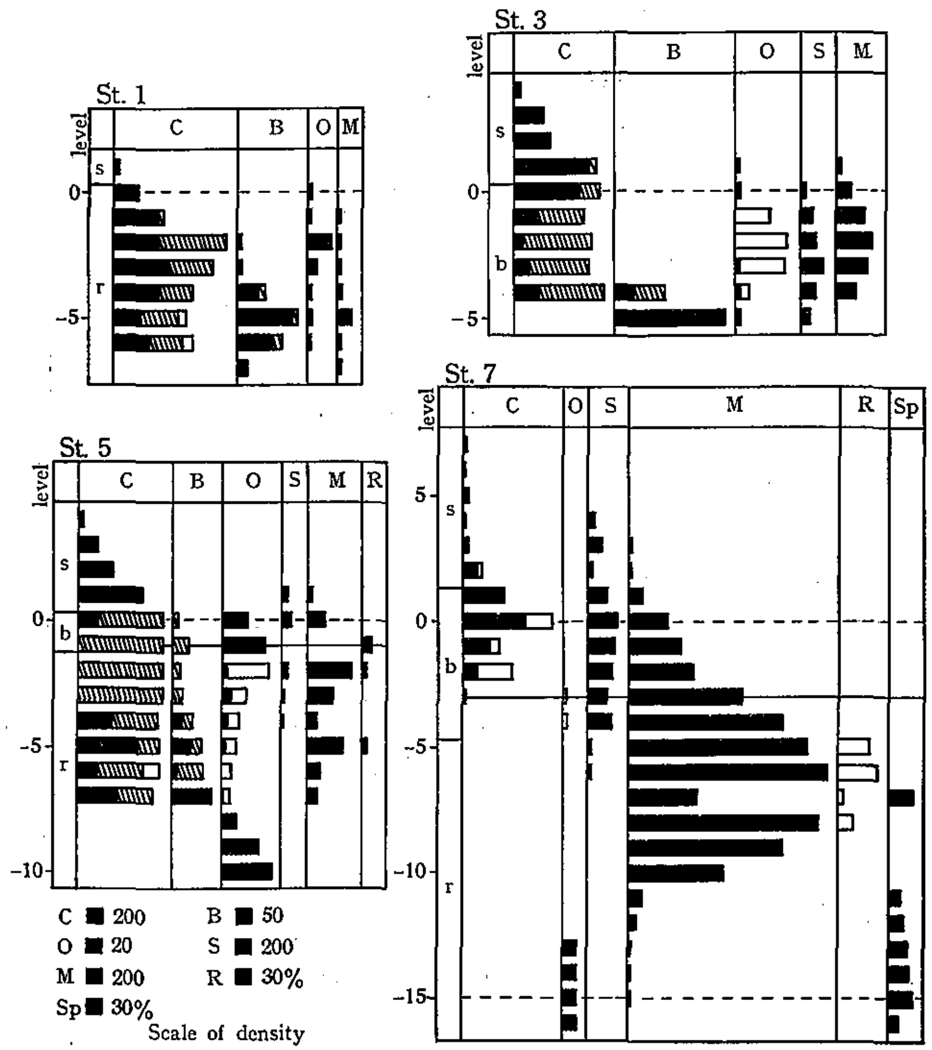

Fig. 1. The vertical distribution of the animals is illustrated with the individual number in a horizontal belt and with the percentage of the covered area to the total area of a belt in the case of two species of porifera. The present number is represented by the black bars, the number covered with *O. gigas* by the shaded bars and that covered with *M. edulis* by the white bars.

The abbreviations used in the figure are the following:

C. - *C. challengeri*, B. - *B. a. albicostatus*, O. - *O. gigas*, S. - *S. virgatus*, M. - *M. edulis*, R. - *R. japonica*, Sp. - Sponge sp. 1.

s. --- splash part, b. --- breaker part, r. --- brushing water part. Unbroken line --- the border line between the wet part and the drought. Broken line in 0 level --- high water level. Broken line in -15 level --- low water level.

divided into the upper and lower strata in St. 5. The lower part of the *C. challengeri* zone becomes narrow in Sts. 3 and 7 where *M. edulis* and *S. virgatus* settle.

2. *B. a. albicostatus* disappears in St. 7.
3. *R. japonica* is not found in St. 7.
4. *O. gigas* distributes continuously in St. 1 but separates into two strata in Sts 3 and 5. Between these strata *M. edulis* dominates and in St. 7 *O. gigas* is found only in the lower part between tide marks.

Furthermore, with respect to each horizontal zone, the percentage of individual number of *M. edulis* in each of the five squares to the total number of the same species in each zone was statistically compared with that of the other species. The following results were obtained from this treatment. Namely, *C. challengeri* decreases in number where *M. edulis* and *S. virgatus* settle abundantly, because the rock face for settlement of *C. challengeri* becomes narrow. It is noted that at the lower part of the *C. challengeri* zone many small spats of *C. challengeri* settle on the shell of mussels resulting in the increasing of individual number.

In the case of *B. a. albicostatus*, the same tendency as in *C. challengeri* is suggested but fewer individuals attach to the shell of bivalves.

In St. 1, *M. edulis* accumulates around the shells of *O. gigas* and by the increase in its individual number *O. gigas* is compelled to form a narrow survival zone there. As usual, *S. virgatus* appears within the clusters of *M. edulis*.

The inversely proportional relation tends to be found between *C. challengeri* and *O. gigas*, for the individual number of *C. challengeri* which attached to the shell of *O. gigas* is less than on the bare rock. At "-7" of St. 1, *B. a. albicostatus* attaches to the rock face where *C. challengeri* does not settle, and the relation between both species is inversely proportional.

It was readily recognized that the inverse relation between *M. edulis* and *O. gigas* was due to that the latter was covered with the former. Therefore, to examine this fact *M. edulis* was removed from the substrata by cutting off the byssus threads. Beneath it there were found shells of *C. challengeri* and *O. gigas* and *R. japonica*. Among these shells blanketed by *M. edulis* all individuals of *C. challengeri* were dead, the majority of *O. gigas* were also dead, though a few of them were still lived, almost all of the dead animals had the two valves intact completely suggesting that *O. gigas* was killed by the blanketing of *M. edulis*.

R. japonica which was found covered with *M. edulis* was living.

Moreover, *C. challengeri* and *B. a. albicostatus* are covered with *O. gigas*. It is supposed that the two species of barnacles were killed by the covering with *O. gigas* judging from that each of them still possessed both tergum and scutum.

The distribution of the animals covered with *M. edulis* is represented by the white bars, and that covered with *O. gigas* by the shaded bars in Fig. 1.

From the above, it is clear that the distribution and the abundance of the barnacles are influenced by *O. gigas* and *M. edulis*. The individual number of barnacles is reduced by the covering of *O. gigas* and *M. edulis*. The present number of *C. challengeri* reaches to half of the initially settled animals in St. 1. In St. 3, the reduction of its population is most remarkable. In St. 5, the initial and continuous *C. challengeri* zone is divided into two strata by the effect of the covering of *O. gigas* in its middle part. *O. gigas* spreads over the bare rock and the shells of barnacles, and then brings about the settling of *M. edulis* and consequently is covered with the latter. The *O. gigas* zone is covered with so many individuals of *M. edulis* in its middle part that *O. gigas* distributes in two separated strata in Sts. 3 and 5. In the upper part of St. 7 the settled *O. gigas* was completely covered with *M. edulis*. From the appearance of *R. japonica* after the removal of *M. edulis* it is evident that a remarkable *R. japonica* zone had been formed in the middle part of St. 7. The covering was not found between two species of barnacles, except for only two cases where two individuals of *B. a. albicostatus* covered some of *C. challengeri*.

DISCUSSION

From the results that the covering phenomena in the course of the formation of zonation are recognized as is mentioned above, it is known that the zonation was not always formed in response of each constituent species to the environmental factors. McDougall (1943) described that three forming processes of zonation are recognized and that larvae settle uniformly but adverse conditions destroy them above and below certain limits. From the results of the present study it seems that the effect of the other species is also one of the adverse conditions. It has been described that the raising of the upper limit of the Balanoid zone and the lowering if the lower limit of it are due to the increase in the intensity of the surf (Moor 1935, Evans 1947). In the present study, in spite of the increase in the intensity of wave action, the lower limit of *C. challengeri* does not become lower in St. 7, and *C. challengeri* distributes in two separated strata in St. 5. The same phenomenon as observed in *C. challengeri* was found also in *O. gigas* in Sts. 3 and 5.

According to Katada and Matsui (1953) the lower limit of one species varies by the effect of the other species which appear successively. However, such phenomenon is observed not only in the lower limit, but also in other parts there appears generally a modification of the zone constituents by the interspecific relation. The lower parts of the *C. challengeri* zone in each station are covered with *O. gigas*, whereas the middle part of the *O. gigas* zone in Sts. 3 and 5, and the upper limit of it in St. 7 were covered with *M. edulis*.

In St. 7 *R. japonica* was completely covered with *M. edulis*.

Stephenson (1939) illustrated the colonization by patches of brown algae in the Balanoid zone. It is noticed by Evans (1949) that modification of the Balanoid zone occurs by the invasion of Fucoid algae, *M. edulis* and others. Hewatt (1935) observed that the denuded rock face was dominated by *Mytilus californianus* after the successive change of settled animals. In the present research it may be said that it is usual that at the first stage *C. challengeri* and *B. a. albicostatus* which settle on the rock are covered first with *O. gigas* and subsequently *O. gigas* is covered with *M. edulis*. But occasionally *C. challengeri* is directly covered with *M. edulis*. It seems that *R. japonica* is directly coverd with *M. edulis*.

SUMMARY

Zonations on the cliff of a headland were studied with special reference to the interrelation of animals.

In the splash water part, there appear *C. challengeri* and *O. gigas*. In the breaker part and brushing water part, the zones consist of *C. challengeri*, *B. a. albicostatus*, *O. gigas*, *S. virgatus*, *M. edulis*, *R. japonica* and Sponge sp. 1.

The distribution of *C. challengeri* and *B. a. albicostatus* is modified by the invasion of *O. gigas*.

It was clarified that the distribution of *C. challengeri*, *B. a. albicostatus*, *O. gigas* and *R. japonica* was modified by the covering of *M. edulis*.

From the obtained results, it is concluded that the covering by other species is one of the important factors in the course of the determination of zonation.

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